The widespread declines of songbirds in rural Britain do not correlate with the spread of their avian predators

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During the last 30 years, there have been marked declines in the populations of many British songbirds breeding on farmland, while two of their main predators, sparrowhawk (*Accipiter nisus*) and magpie (*Pica pica*), have spread back into areas from which they had disappeared. The causes of the songbird declines remain unclear but given the coincidence in timing, it might appear that increased predation could be responsible. Although many studies have failed to find links between changes in the populations of breeding songbirds and mortality from avian predators, previous work has, with few exceptions, involved only short-term studies on small spatial scales. Here we use large-scale, long-term data from a national bird census scheme to examine whether magpies and sparrowhawks could have depressed the rates of year-to-year population change in 23 songbird species. Our results indicate that magpies and sparrow-hawks are unlikely to have caused the songbird declines because patterns of year-to-year population change did not differ between sites with and without these predators.

Keywords: predation; population declines; rates of population change

1. INTRODUCTION

Research into the role of predators in regulating the distribution and abundance of organisms has been characterized by considerable controversy. Perceived conflict between the interests of nature conservationists and those involved in game-shooting has made the effect of predators on bird populations a particularly contentious issue (Newton 1993). Adding to the controversy, there have been marked and largely unexplained declines in the populations of many British songbirds over the last three decades, and while these have coincided with wide-ranging changes in agricultural practices, they have also coincided with large-scale expansions in the populations of predatory magpies and sparrowhawks (Marchant *et al.* 1990; Fuller *et al.* 1995; Gibbons *et al.* 1996). It might seem unlikely that these population declines could have been driven by predation from magpies and sparrowhawks: many studies have failed to find effects of avian predators on songbird populations (Newton 1993), but apart from a small number of studies (Gooch *et al.* 1991; Newton *et al.* 1997), these have been short-term and small-scale. Here we aim to study whether magpies and sparrowhawks affect the rates of population change in a wide range of songbird species using large-scale long-term data from a national bird census scheme.

2. METHODS

(a) *The common birds census*

The common birds census (CBC) (Marchant *et al.* 1990) has monitored breeding bird numbers since 1962 (table 1; figure 1). Volunteers have visited around 200 woodland and farmland CBC plots ten times each year to map bird territories (Marchant *et al.* 1990). The CBC covered the period when sparrowhawks spread eastward into intensive arable farming areas as many of the organochlorine pesticides which had caused their elimination were withdrawn progressively from use (Newton & Haas 1984). It also covered the period when the number of lowland gamekeepers declined and magpies too spread east (Gregory & Marchant 1995). The CBC therefore offers an exceptionally large-scale long-term data set with which to look for correlations between the presence of predators at individual sites in individual years and the rates of songbird population change at these sites between consecutive years. It provides an excellent opportunity to look for a link between the declines of British songbirds and the expansion of magpie and sparrowhawk populations. We examined 23 species censused by the CBC; all of these are taken as prey by sparrowhawks (Newton 1986), and the nests of many are also vulnerable to magpies which eat eggs and nestlings (Birkhead 1991).

For each of these songbirds, we compared inter-annual changes in the territory counts between individual plots where each predator was or was not recorded at least once during the season. There were three reasons why we used this presence–absence measure rather than territory counts for the predators. First, we wanted to include potential effects of non-breeding predators. Second, sparrowhawks are elusive and may only be seen a few times even when holding territory. Third, although

Figure 1. Using 1970 and 1990 as example years, these maps show the locations of CBC plots on which each predator was recorded (filled circles) and those on which they were not recorded (open circles). The patterns of occupied and unoccupied plots illustrate the spread of these predators through Britain during the study period (1965–1995). For the two example years shown, the maps include only those plots used in the analysis. (*a*) Sparrowhawk 1970; (*b*) sparrowhawk 1990; (*c*) magpie 1970; (*d*) magpie 1990.

breeding magpies are conspicuous, it is difficult to count them reliably when they occur at high densities. Because of the large number of plots and years, potential effects of magpies and sparrowhawks are not confounded and can readily be distinguished.

Few plots have been censused throughout our entire study period (1965–1995), but we used data from plots where standard census methods yielded at least seven measures of inter-annual rates of population change. Thousands of data points were available for many of the 23 songbird species studied (table 1). These species had a range of body sizes, diets, habitat requirements and migratory behaviour (Snow & Perrins 1998). They included hole-nesting species, whose eggs and nestlings are mostly protected from magpie predation, and open-nesting species. Many showed marked population declines over the study period but some remained stable, or increased (Crick *et al.* 1998).

(b) *Analytical methods*

We conducted our analysis in two stages. First, given that the national declines of many songbirds appear to have coincided with the national expansions of the magpie and sparrowhawk populations, we looked for simple statistical relationships between rates of songbird population change on individual CBC plots and the presence or absence of each predator on each plot in each year (model R). However, because independent changes in both predator and prey populations could cause spurious statistical correlations, we then corrected for nationwide changes in rates of songbird population change and looked at whether rates of songbird population change still differed between plots with and without predators (model R_t). This second stage allowed us to examine whether, at any given time, rates of songbird population change were lower on plots where predators were seen than on plots where they were not seen.

(i) *The population model*

Analyses were based on the population model

$$\log_e (\mathcal{N}_{t+1,i}/\mathcal{N}_{t,i}) = R[or\ R_t] + a\,(S_{t,i}) + b(H_{t,i}) + c(M_{t,i})$$

where $\mathcal{N}_{t,i}$ is the abundance of songbird territories in year t on plot i, R [or R_t] is the expected value of $\log_e(\mathcal{N}_{t+1,i}/\mathcal{N}_{t,i})$ [in year t] in the absence of predation and intraspecific competition; $H_{t,i}$ and $M_{t,i}$ are dummy variables indicating the presence (1) or absence (0) of sparrowhawks and magpies, respectively, on plot i in year t; b and c are the amounts by which $\log_e(\mathcal{N}_{t+1,i}/\mathcal{N}_{t,i})$ is reduced if sparrowhawks and magpies, respectively, are present. (The same conclusions were reached when each predator was studied separately (method 2; table 2), when $H_{t+1,i}$ and $M_{t+1,i}$ were used in place of $H_{t,i}$ and $M_{t,i}$, and when sparrowhawk and magpie counts were used in place of $H_{t,i}$ and $M_{t,i}$.)

(ii) *Accommodating density dependence, standardizing abundance*

Because density dependence might otherwise mask effects of predators, we included $S_{t,i}$ (a standardized measure of songbird abundance on each plot) in the model. Although a is nominally the amount by which $\log_e(\mathcal{N}_{t+1,i}/\mathcal{N}_{t,i})$ is reduced below R [or R_t] for each unit of standardized songbird abundance, the estimate of a is also known to be influenced by measurement error in songbird counts (Wolda & Dennis 1993). This approach does not therefore provide a formal means of testing statistically for density dependence but it is a parsimonious way of accommodating any density dependence while focusing on the effects of the predators.

When allowing for density dependence, we standardized songbird numbers by dividing by the average abundance counted on the plot across all years to correct for differences in the size and habitat quality of CBC plots. Because of population trends however, the average songbird abundance also depends on the run of years over which birds on the plot is censused, so we used the techniques of Ter Braak *et al.* (1994) to produce a mean national population index for the census period and multiplied by this.

We considered this two-stage standardization procedure (method 1, table 2) to be the most appropriate, but we tried other methods to check our conclusions were robust. In method 3 we only divided the annual counts by the average count for the plot and did not incorporate the national index values. In method 4 we did not standardize songbird abundances at all. Instead, using plots with at least 12 measures of songbird population change, we avoided the problem of differences in plot size and quality by fitting a model that estimated the effects of songbird, sparrowhawk and magpie abundances on the rate of population change using separate estimates of parameters analogous to a, b and c for each plot, while keeping R or R_t common across plots. Across all methods (table 2), model R yielded several significant correlations between the rate of songbird population change and the presence of predators, but model R_t yielded no more than would be expected by chance. In other words, all methods pointed to the conclusion that predators did not affect rates of songbird population change.

(iii) *Implementing the analyses*

Using $\mathcal{N}_{t+1,i}$ as the dependent variable, we fitted generalized linear models in SAS PROC GENMOD (SAS Institute 1996) using Poisson errors and a log link function. We excluded all cases where $\mathcal{N}_{t,i}=0$ because $\log_e\mathcal{N}_{t,i}$ was fitted as an offset (i.e. an explanatory variable with a fixed coefficient of 1). We estimated R by fitting an intercept, and R_t by fitting year as a factor. $S_{t,i}$, $H_{t,i}$ and $M_{t,i}$ were the independent variables. For methods 1, 2 and 3, Wald χ^2-tests (adjusted for overdispersion with the DSCALE option (SAS Institute 1996)) were used to test whether b and c differed from zero. With method 4, we used a binomial sign test to examine whether the frequencies of negative values for b and c differed from those expected by chance.

(c) *Statistical power*

Although the second stage of the analysis (model R_t) involved the estimation of more parameters from the data, and although this could under some circumstances reduce the precision with which the parameters of interest, b and c, are estimated, we checked that in practice the data were sufficiently abundant for this not to be a problem. We evaluated changes in the precision of the estimates of b and c by comparing their standard errors between the R and the R_t model for each species.

(d) *Spurious correlations with non-predatory birds*

To examine further the possibility that independent but coincident national population changes could give rise to spurious correlations between rates of songbird population change and the presence of predators, we repeated the analysis replacing the data on the predators with data on collared doves *Streptopelia decaocto* which are not predators of songbirds. Collared doves expanded their range during the same period as magpies and sparrowhawks, but they spread from the east rather than from the west (Marchant *et al.* 1990).

Table 1. *Sample sizes, population trend (Crick et al. 1998), and results of analyses which did (R_t) and did not (R) control for nationwide variation in rates of population change*

species	N[a]	no. of plots	trend[b]	R hawk b (s.e.)	R magpie c (s.e.)	R collared dove d (s.e.)	R_t hawk b (s.e.)	R_t magpie c (s.e.)	R_t collared dove d (s.e.)
Alauda arvensis	2048	157	decrease	**−0.084 (0.0150)***	**−0.069 (0.0146)***	**−0.065 (0.0130)***	0.016 (0.0148)	−0.009 (0.0138)	**0.028 (0.0130)***
Anthus pratensis	844	65	decrease	−0.045 (0.0269)	−0.017 (0.0255)	**−0.065 (0.0291)***	−0.001 (0.0283)	−0.003 (0.0262)	−0.020 (0.0293)
Troglodytes troglodytes	3743	286	stable	0.003 (0.0112)	−0.030 (0.0165)	−0.014 (0.0108)	0.006 (0.0097)	**−0.028 (0.0135)***	0.003 (0.0092)
Prunella modularis	3649	278	decrease	**−0.088 (0.0112)***	**−0.047 (0.0139)***	**−0.077 (0.0103)***	−0.015 (0.0112)	0.002 (0.0131)	0.007 (0.0105)
Erithacus rubecula	3751	289	stable	−0.0003 (0.0089)	−0.018 (0.0129)	−0.004 (0.0086)	−0.004 (0.0088)	−0.022 (0.0122)	0.008 (0.0084)
Turdus merula	3874	294	decrease	**−0.050 (0.0073)***	**−0.028 (0.0095)***	**−0.049 (0.0068)***	−0.007 (0.0074)	0.004 (0.0092)	−0.004 (0.0070)
Turdus philomelos	3623	276	decrease	**−0.112 (0.0139)***	**−0.043 (0.0151)***	**−0.110 (0.0125)***	**−0.030 (0.0131)***	0.007 (0.0138)	−0.008 (0.0123)
Turdus viscivorus	2606	202	decrease	−0.033 (0.0183)	**−0.072 (0.0265)***	**−0.064 (0.0176)***	**0.037 (0.0189)***	−0.013 (0.0263)	−0.009 (0.0185)
Phylloscopus collybita	2190	178	increase	−0.002 (0.0177)	−0.030 (0.0309)	**−0.047 (0.0171)***	0.009 (0.0168)	−0.015 (0.0286)	0.003 (0.0166)
Phylloscopus trochilus	3368	264	stable	**−0.023 (0.0108)***	−0.013 (0.0128)	−0.008 (0.0106)	0.003 (0.0110)	0.004 (0.0124)	0.020 (0.0109)
Parus ater[c]	2033	164	increase	−0.023 (0.0183)	−0.011 (0.0228)	−0.029 (0.0184)	−0.003 (0.0185)	−0.010 (0.0223)	−0.010 (0.0185)
Parus caeruleus[c]	3741	285	increase	0.010 (0.0080)	−0.009 (0.0116)	**0.017 (0.0077)***	−0.0004 (0.008)	−0.013 (0.0116)	0.009 (0.0080)
Parus major[c]	3643	278	stable	**0.031 (0.0101)***	0.003 (0.0150)	**0.021 (0.0098)***	0.011 (0.0106)	−0.010 (0.0149)	0.003 (0.0101)
Sitta europaea[c]	1035	86	increase	0.025 (0.0258)	0.011 (0.0375)	**0.061 (0.0250)***	0.006 (0.0260)	−0.013 (0.0383)	0.037 (0.0256)
Sturnus vulgaris[c]	1156	105	decrease	−0.044 (0.0286)	**−0.069 (0.0345)***	**−0.103 (0.0264)***	0.045 (0.0313)	−0.023 (0.0344)	−0.039 (0.0302)
Passer montanus[c]	1000	86	decrease	**−0.196 (0.0468)***	−0.038 (0.0340)	**−0.109 (0.0310)***	−0.054 (0.0475)	0.003 (0.0321)	0.017 (0.0338)
Fringilla coelebs	3763	287	increase	**0.023 (0.0071)***	0.002 (0.0089)	**0.026 (0.0070)***	0.004 (0.0074)	−0.011 (0.0089)	0.008 (0.0073)
Carduelis chloris	2723	217	stable	**−0.058 (0.0179)***	−0.020 (0.0203)	**−0.072 (0.0161)***	−0.014 (0.0195)	0.016 (0.0206)	−0.008 (0.0185)
Carduelis carduelis	1786	146	stable	−0.033 (0.0254)	**−0.081 (0.0347)***	−0.041 (0.0253)	0.042 (0.0264)	−0.019 (0.0333)	0.037 (0.0273)
Carduelis cannabina	2234	172	decrease	**−0.093 (0.0219)***	−0.037 (0.0233)	**−0.076 (0.0189)***	−0.007 (0.0227)	0.026 (0.0229)	0.013 (0.0200)
Pyrrhula pyrrhula	2645	212	decrease	**−0.109 (0.0182)***	−0.036 (0.0265)	**−0.042 (0.0174)***	−0.026 (0.0186)	0.017 (0.0258)	0.017 (0.0177)
Emberiza citrinella	2471	191	decrease	**−0.048 (0.0133)***	−0.027 (0.0165)	−0.017 (0.0125)	−0.007 (0.0140)	0.002 (0.0166)	0.021 (0.0134)
Emberiza schoeniclus	1350	104	decrease	**−0.097 (0.0244)***	−0.040 (0.0279)	**−0.057 (0.0211)***	−0.018 (0.0276)	0.009 (0.0276)	0.006 (0.0226)

[a] The number of observations of the rate of inter-annual songbird population change.

[b] Species categorized as either increasing or decreasing have shown at least a 25% net change in population size during the period 1972–1996 (Crick *et al.* 1998).

[c] Hole-nesting species whose eggs and chicks are therefore mostly protected from magpies.

Values shown are the amounts by which $\log_e(N_{t+1,i}/N_{t,i})$ is affected by the presence of each of the predators, i.e. negative values show that the rate of population change is lower when predators are present. Standard errors are shown in brackets. These are the results before significance levels were corrected for multiple tests. The significant correlations in R_t should not be regarded as showing a causal effect of predation because none is significant after correcting for multiple tests.
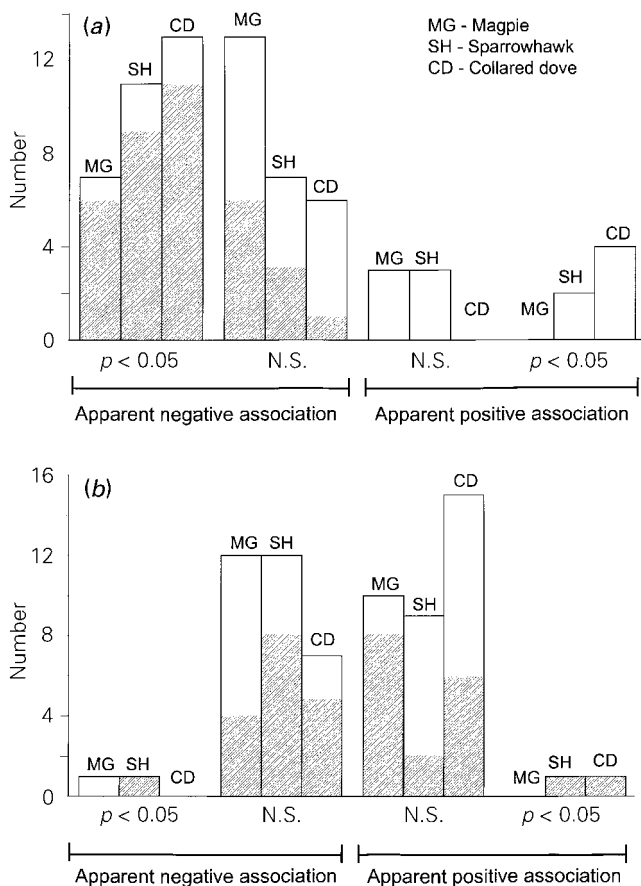
* Significant results are in bold and asterisked.

Figure 2. Numbers of species showing significant relationships between rates of population change and the presence of magpies, sparrowhawks or collared doves, before (*a*) and after (*b*) controlling for nationwide variation in the rate of songbird population change. Cross-hatching indicates numbers of declining species in each group (table 1). This figure shows the results before the significance levels were corrected for multiple tests. Results are only shown for method 1 (see §2.) although we checked that the same conclusions were reached with slightly different analytical techniques.

3. RESULTS

(a) *Model R*

In the first stage of the analysis (model *R*), from 46 possible correlations we found seven statistically significant relationships between rates of songbird population change and the presence of magpies and 13 significant relationships with the presence of sparrowhawks (table 1; figure 2*a*). Of these, 11 relationships (all negative) were still significant after the Bonferroni method was used to correct for multiple tests. There were more negative than positive relationships (figure 2*a*), mainly because of correlations with declining species.

Similar correlations were found with the presence of collared doves, demonstrating that these patterns could reflect independent but coincident population changes, rather than causal effects of predation (table 1; figure 2*a*).

(b) *Model R_t*

In the second stage of the analysis (model R_t), by including year as a factor in the models, we controlled for other environmental changes that could affect bird popu-

Table 2. *Numbers of species where positive, negative, and nonsignificant correlations between rates of population change and predators were found with different methods*

			R			R_t	
		−ve	n.s.	+ve	−ve	n.s.	+ve
method 1	hawk	11	10	2	1	21	1
	magpie	7	16	0	1	22	0
method 2	hawk	13	8	2	1	22	0
	magpie	11	12	0	1	22	0
method 3	hawk	8	15	0	0	23	0
	magpie	4	19	0	2	21	0
method 4	hawk	2	20	1	1	21	1
	magpie	8	14	1	2	20	1

Model R_t controls for nationwide yearly variation in rates of interannual songbird population change, whereas model *R* does not. Note that our conclusions are robust because results are consistent across methods—numerous correlations can be found in model *R*, but not in model R_t—so although some songbirds declined as predators spread, declines were not more marked on plots with predators. The details of these methods are outlined in §2. These are the results before significance levels were corrected for multiple tests.

lations and tested whether rates of population change still differed between plots with and without predators. In this second stage, from the 46 possible correlations examined, we found only three significant relationships (two negative and one positive) between rates of songbird population change and predators (table 1; figure 2*b*), and none of these were significant when the Bonferroni method (Sokal & Rohlf 1995) was used to allow for multiple testing. A similar correlation was found with collared doves (table 1; figure 2*b*).

(c) *Statistical power*

We verified that the smaller number of significant correlations in the second analysis (model R_t) did not result from a marked increase in the standard errors of *b* and *c*, but from reductions in the magnitudes of *b* and *c* themselves. The standard error of *b* (sparrowhawk effect) increased by an average of only 0.000499 (mean change = +2.1% of s.e. for model *R*; range −13.6% to +13.1%) and that of *c* (magpie effect) actually declined by 0.000576 (mean = −3.0%, range −18.1% to +2.8%).

4. DISCUSSION

Although the population declines of many songbird species coincided with the spread of both magpies and sparrowhawks through rural Britain, and although this in itself can give rise to statistical relationships between rates of songbird population change and the presence of predators on individual plots, the population declines have also coincided with other long-term large-scale changes such as the spread of collared doves, and rates of songbird population change correlate with these too. At any given time, geographical variation in the rate of songbird population change was not related to the presence of sparrowhawks or magpies.

There is good evidence that predators can affect gamebird populations (Newton 1993; Tapper *et al.* 1996; Redpath & Thirgood 1997), and it could be that magpies

and sparrowhawks have effects on populations of breeding songbirds in a few species or in some specific localities, but our analyses did not support the idea that these predators have depressed the national populations of the species studied here. The precise causes of the songbird declines mostly remain unclear but, since there is extensive evidence that the declines are a feature of farm-land habitats (Fuller *et al.* 1995; Siriwardena *et al.* 1998), it would be prudent to focus attention on the consequences of agricultural intensification (O'Connor & Shrubb 1986; Campbell *et al.* 1997; Pain & Pienkowski 1997; Wilson *et al.* 1997).

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